

A Review of the Host Ranges of Aphidophagous Aphelinidae (Hymenoptera: Chalcidoidea)

ROBERT L. ZUPARKO

Center for Biological Control, University of California, Berkeley, 1050 San Pablo Avenue,
Albany, California 94706

Abstract.—The genera *Protaphelinus* and *Aphelinus* (the latter divided into three subgenera) comprise all known aphidophagous Aphelinidae. A literature review indicates that these four formal superspecific taxa are largely restricted to hosts in different families: *Protaphelinus* on Pemphigidae, *Aphelinus* (*Indaphelinus*) on Greeneidae, *Aphelinus* (*Mesidia*) on Drepanosiphidae, and *Aphelinus* (*Aphelinus*) on Aphididae.

INTRODUCTION

Until 1972, the aphidophagous species of Aphelinidae (Hymenoptera: Chalcidoidea) were divided into three genera, *Aphelinus* Dalman, *Mesidia* Foerster and *Mesidiopsis* Novicky. Records of *Marietta* Motschulsky reared from aphids (Viggiani 1984) refer to incidences of hyperparasitism only. Species from *Aphelinus* are recorded from Aphididae, Drepanosiphidae, Lachnidae, Pemphigidae, Thelaxidae (all Homoptera), plus several non-homopteran hosts (Peck 1963, Ferrière 1965, Nikol'skaya and Jasnosh 1966, Kalina and Stary 1976). Lagace (1969a) noted that *Mesidia* was apparently restricted to the Phyllaphidini (Homoptera: Drepanosiphidae), while the sole species in *Mesidiopsis*, *M. subflavescens* (Westwood) was known only from arboreal Drepanosiphidae (Ferrière 1965).

Mackauer (1972) erected *Protaphelinus*, in which he placed *A. nikolskajae* Jasnosh, known only from Pemphigidae. *Mesidiopsis* and *Mesidia* were synonymized with *Aphelinus* by Boucek and Graham (1978) and Hayat (1983) respectively. Hayat (1990) divided *Aphelinus* into three subgenera: *Indaphelinus* (for a single yellow-bodied species), *Mesidia* (for the remaining

yellow-bodied species), and *Aphelinus* (for the dark-bodied species).

I have reared several *Aphelinus* species from aphids in northern California (Zuparko 1983, Zuparko and Dahlsten 1993, Zuparko and Dahlsten 1995, Appendix). Most of these species are sympatric and share the same general ecological habitat (deciduous urban shade trees), but I found species assigned to *A. (Mesidia)* tended to attack drepanosiphids, and those classified in *A. (Aphelinus)* preferred aphidids. This led me to conduct a literature review of the aphidophagous aphelinids to determine if a similar pattern occurred on a larger scale.

The two most extensive listings of *Aphelinus* host records previous to this are found in Peck's (1963) catalog of Nearctic Chalcidoidea and in Kalina and Stary's (1976) review of the hosts of European *Aphelinus*. Both studies predate the synonymization of *Mesidia* and *Mesidiopsis*, and do not include taxa from Africa and Asia. Additionally, at least 11 new species have been described in *Aphelinus* since these works.

METHODS

I used only host records that could be assigned to a specified family of aphids,

excluding records such as "aphis" or "aphids" and specific names of questionable taxonomic status. I consider records of non-aphid hosts doubtful, and excluded them as well. I used Heie's (1980) system of aphid classification, and followed Eastop and Hille Ris Lambers (1976) and Smith and Parron (1978) for aphid synonymies and placement.

This work is not meant to validate any aphelinid at the specific level: I largely accepted the taxa defined by Mackauer (1972), Graham (1976), Kalina (1976), Gordh (1979), Wharton (1983), Polaszek and Hayat (1989), Hayat (1990) and Prinsloo and Naser (1994). The only exception is my consideration of *A. asychis* Walker. The synonymization of this species with *A. semiflavus* Howard (Ferrière 1965) tends to confuse records of populations that were disjunct until the mid-1900's, when Old World material was imported to North America in a series of biological control programs (van den Bosch 1957, Simpson et al. 1959, Jackson et al. 1971). Although *A. asychis* and *A. semiflavus* may be conspecific, I treat this group as three taxa based on their separation before these introductions: 1). *A. asychis* "NA", endemic to North America (= *A. semiflavus* in pre-1970 literature), 2). *A. asychis* "Eur", native to Europe and imported to North America for control of *Schizaphis graminum* (Rondani) and other Aphididae in the 1970's, and 3). *A. asychis* "Israel" (= *A. semiflavus* in early reports), imported to North America from Israel and the Middle East for control of a drepanosiphid, *Therioaphis maculata* (Buckton), in the 1950's.

RESULTS

Host records are summarized in Table 1. The two described species in *Protaphelinus* and *A. (Indaphelinus)* are known only from Pemphigidae and Greeneidae, respectively. Of the 55 host records for *A. (Mesidia)*, 50 (91%) were from Drepanosiphidae, and 5 from Aphididae.

Of the 302 host records for *A. (Apheli-*

nus), 273 (90%) were from Aphididae. The remaining were from Drepanosiphidae (16), Pemphigidae (10), Hormaphididae (1), Lachnidae (1) and Thelaxidae (1). Of the 35 taxa with recorded hosts in this subgenus, 27 (77%) are known exclusively, and 5 (14%) primarily, from Aphididae.

DISCUSSION

The taxonomy of *Aphelinus* is not yet well elucidated. Zehavi and Rosen (1988) discussed an "*A. mali* group" whose members share similar morphological characters, but proposed no formal subdivisions of the genus. Hayat's (1990) concept of subgenera is based primarily on the Nearctic and western Palearctic fauna; only four species of *Aphelinus* have been described from Africa and three from eastern Asia (two of which are unplaced to subgenus).

Flanders (1953) stressed the importance that biological characters can provide with regard to the taxonomy of aphelinids. Hagen and van den Bosch (1968) speculated on the relationship of aphid morphology with parasitoid host selection, while Mackauer (1965) proposed using aphid/parasitoid host records of Aphidiinae (Hymenoptera: Braconidae) to help elucidate aphid phylogeny. Haardt and Holler (1992) reported differences in rates of parasitism and development in six European isofemale lines of *A. abdominalis* (Dalman), and found three groups that appeared to be reproductively isolated.

The results of this survey form a pattern of host specificity which supports the superspecific classifications proposed by Mackauer (1972) and Hayat (1990): each superspecific taxon is largely restricted to a different host family—*Protaphelinus* to Pemphigidae, *Aphelinus (Indaphelinus)* to Greeneidae, *A. (Mesidia)* to Drepanosiphidae and *A. (Aphelinus)* to Aphididae. Of the 69 taxa treated in this paper, 12 had unrecorded hosts, and a further three were *Aphelinus* species unplaced to sub-

genus, but of the remaining 54 species, 41 (76%) followed this pattern exactly.

Ten taxa largely conformed to this pattern, but had a total of 19 conflicting host records. Nine of these records (from *A. automatus* Girault, *A. fulvus* Jasnosh, *A. gilletti* (Howard), *A. sp. nr. perpallidus* Gahan, *A. abdominalis*, *A. chaonia* Walker and *A. semiflavus*) were based on rearings of less than 10 specimens each, and a further five (of *A. asychis*) are known only from laboratory exposures.

Although these records document a physiological ability to reproduce in a variety of hosts, the rarity of the field rearings suggests they are atypical parasitizations and do not reflect a parasitoid's normal life history. The physiological restrictions on *Aphelinus* host ranges have not been clearly delineated. Wilbert (1964) reported that *A. asychis* would attack drepanosiphids and aphidids, but not a pemphigid or a phylloxerid, while Carver and Woolcock (1985) demonstrated that *A. asychis* parasitized several genera of Aphididae, but failed to successfully develop in several others due to encapsulation and host incompatibility. Jackson and Eikenbary (1971) and Raney et al. (1971) suggest morphological or behavioral characters may be important aphid defense mechanisms which could influence aphelinid host choices.

Previous lab studies generally support the noted pattern of host ranges. Mackauer and Finlayson (1967) remarked on the absence of *A. asychis* "NA" (= *A. semiflavus*) from *Therioaphis* species in the field, and were unable to transfer it to *T. riehmii* (Borner) in the lab. Another drepanosiphid, *Periphyllus negundinis* (Thomas), was accepted for oviposition, but all parasitoids died before emerging. Transfers to aphidid species were generally successful. Jackson and Eikenbary (1971) and Raney et al. (1971) found that *A. asychis* demonstrated a distinct non-preference for the drepanosiphid *Siphia flava* (Forbes); the latter group of workers doubted the ability

of *A. asychis* to survive on this aphid in the field. Wood (1958) reported *A. varipes* (Foerster) (as *A. nigrinus*) attacked four species of Aphididae, but not a drepanosiphid or a fifth aphidid species.

I found only three taxa did not follow this pattern of host specificity: all are in *Aphelinus* (*Aphelinus*), and are relatively more host specific (apparently to a single species or genus) than are the majority of the species in their subgenus. *Aphelinus mali* has been recorded from many species of Aphididae, but is most often found on the pemphigid *Eriosoma lanigerum* (Hausmann). Howard (1929) thought *A. mali* was restricted to aphids with waxy coverings (mostly Pemphigidae) and that other records were misidentifications. Michel (1969) and Kalina and Stary (1976) considered *A. mali* was specific to *E. lanigerum*. In lab trials, Zehavi and Rosen (1988) found that *A. mali* attacked *E. lanigerum* and ignored *Aphis gossypii* Glover (an acceptable host according to Howard [1895]), whereas *A. paramali* Zehavi and Rosen (which closely resembles *A. mali*) exhibited exactly the opposite behavior. *Aphelinus prociphili* Carver has been recorded only from a pemphigid (Carver 1980). This species was placed in the "*A. mali* group" (Zehavi and Rosen 1988). In the field, *Aphelinus asychis* "Israel" has been reared only from *Therioaphis* species, though Finney et al. (1960) found it "readily attacked" *Myzus persicae* (Sulzer) (Aphididae) in the lab. Manglitz and Schalk (1970) reported very low parasitism rates (3%) on *M. persicae*, versus 94% on *T. riehmii*.

Five described *Aphelinus* species have not been placed in Hayat's subgeneric scheme. Hayat (1991b) described *A. nepalensis* without referring it to a subgenus, but noted that it was the most distinctive species in the genus; its host is unknown. *Aphelinus ceratovacunae* Liao was described from eastern Asia (Liao et al. 1987), but its subgeneric placement is unknown. Its rearing from the Hormaphididae (Ho-

Table 1. Number of recorded host aphid species for *Protaphelinus* and *Aphelinus*.

Genus (subgenus)	Species	Aphid host family*							
		Unk	Pem	Hor	The	Dre	Gre	Aph	Lac
<i>Protaphelinus</i>	<i>nikolskajae</i>		5						
	sp.	X							
<i>Aphelinus</i> (<i>Indaphelinus</i>)	<i>ancer</i>						1		
<i>Aphelinus</i> (<i>Mesidia</i>)	<i>annulipes</i>					3			
	<i>argiope</i>					3			
	<i>aureus</i>					3			
	<i>automatus</i>					3		1	
	<i>fulvus</i>					1		1	
	<i>gilletti</i>							1	
	sp. nr. <i>gilletti</i>					1			
	<i>maculatus</i>	X							
	<i>paoliellae</i>					1			
	<i>perpallidus</i>					6			
	sp. nr. <i>perpallidus</i>					1		1	
	<i>subflavescens</i>					17		1	
	sp. nr. <i>subflavescens</i>					4			
	<i>thomsoni</i>					4			
	<i>tetrataenion</i>	X							
	4 unidentified spp.					4			
<i>Aphelinus</i> (<i>Aphelinus</i>)	<i>abdominalis</i>				1			40	
	sp. nr. <i>abdominalis</i>							8	
	<i>albipodus</i>	X							
	<i>asychis</i> "Eur"					7		35	
	<i>asychis</i> "Israel"					4		1	
	<i>asychis</i> "NA"					2		21	
	sp. nr. <i>asychis</i>							1	
	<i>campestris</i>	X							
	<i>certus</i>	X							
	<i>chaonia</i>					2		40	1
	<i>confusus</i>							3	
	<i>daucicola</i>							11	
	<i>desantisi</i>							1	
	<i>dies</i>	X							
	<i>flaviventris</i>							3	
	<i>gossypii</i>							10	
	<i>howardii</i>							8	
	<i>humilis</i>							10	
	<i>hyalopteraphidis</i>							1	
	<i>jucundus</i>							5	
	<i>lapisligni</i>							2	
	<i>maidis</i>							3	
	<i>mali</i>		9	1				16	
	sp. nr. <i>mali</i>							1	
	<i>mariscusae</i>							1	
	<i>meridionalis</i>							4	
	<i>nox</i>	X							
	<i>paramali</i>							8	
	<i>prociphili</i>		1						
	<i>sanborniae</i>							2	
	sp. nr. <i>sanborniae</i>							1	
	<i>siphonophorae</i>							1	
	<i>subauriceps</i>	X							

Table 1. Continued.

Genus (subgenus)	Species	Aphid host family*							
		Unk	Pem	Hor	The	Dre	Gre	Aph	Lac
	<i>toxopteraphidis</i>							2	
	2 spp. nr. <i>toxopteraphidis</i>							5	
	<i>varipes</i>					1		18	
	sp. nr. <i>varipes</i>							2	
<i>Aphelinus</i> "own group"	<i>japonicus</i>	X							
<i>Aphelinus</i> unplaced	<i>ceratovacunae</i>			1					
	<i>marlatti</i>							1	
	<i>nepalensis</i>	X							
	<i>nigra</i>					2			

* Unk = Unknown; Pem = Pemphigidae; Hor = Hormaphididae; The = Thelaxidae; Dre = Drepanosiphidae; Gre = Greeneidae; Aph = Aphididae; Lac = Lachnidae.

moptera) is unusual among *Aphelinus* and suggests it may belong to a separate group. The Hormaphididae is primarily an Oriental family (mainly on bamboos and palms) (Blackman and Eastop 1984) with few other recorded parasitoids, providing a diverse potential host resource. Hayat (1990, 1991a) considered *A. japonicus* Ashmead (also from eastern Asia and its host unknown) did not belong in any of the three subgenera, and placed it in its own species-group.

Aphelinus marlatti (Ashmead) was unplaced to subgenus by Hayat (1990), although Polaszek and Hayat (1989) noted that it appeared to be closest to *A. asychis* and *A. mariscusae* (Risbec), both in the subgenus *Aphelinus*. The only specific host reference is in McLeod (1938), who noted that local populations obtained from an "unidentified species of aphid on cineraria" were successfully reared on *Myzus persicae*.

The placement of *A. nigra* (Lagace) is also problematic. It has been reared from two drepanosiphid genera (Lagace 1969a, Hennessey 1981 [N.B. the latter record should read *Sipha flava* instead of *Siphaf-lava* sp.]), allying it with *A. (Mesidia)*. This species was first described in *Mesidia* based on antennal characters, but differs from other members of this genus by col-

or, discal cilia, and shape of the funicular segments (Lagace 1969a). Additionally, its ovipositional habits are unique for the genus: females oviposit while standing on, instead of next to, the host (Lagace 1969b). This behavior is similar to that of members of the aphelinid genus *Aphytis*, whose separation from *Aphelinus* was based largely on the difference in metasomal morphological features and ovipositional habits (Timberlake 1924, Compere 1955). Kalina and Stry (1976) noted that such characters may have a significant effect in determining host selection. These morphological and biological characteristics may ultimately justify placement of *A. nigra* outside of *Aphelinus*.

Kalina and Stry (1976) argued that aphelinid host ranges are habitat dependent, and other workers have commented on the crucial roles environmental factors play in the survival and reproduction of *Aphelinus* species (Hagen and van den Bosch 1968, Michel 1969, Schlinger and Hall 1959, van den Bosch et al. 1964). The correlation of aphelinid taxa with different aphid families suggests these host ranges reflect a history of coevolution. The most primitive aphid group (Adelgoidea) has no record of aphelinid parasitoids. The Pemphigidae, Drepanosiphidae and Greeneidae represent successively more de-

rived groups (Heie 1987), and each is attacked by a different taxon of aphelinids. The Aphididae is the most recent and diverse aphid family, and is parasitized by the most diverse *Aphelinus* subgenus. This hypothesis may be tested by a phylogenetic analysis of the aphidophagous Aphelinidae. Although such information is not yet available, an analysis of the Aphelinidae is currently in progress (J. Woolley, pers. comm.).

ACKNOWLEDGMENTS

I am most grateful to Ken Hagen for his many crucial and insightful comments during the development of this paper. I also thank Leo Caltagirone, Dan Sullivan, and two anonymous reviewers for their helpful suggestions.

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APPENDIX

New *Aphelinus* spp. host records, 1990-94. (All collections made by R. L. Zuparko). All material deposited in the Essig Museum of Entomology, University of California, Berkeley.

Aphelinus automatus Girault

CALIFORNIA. ALAMEDA CO.: Berkeley; *Myzocallis* sp. on *Quercus agrifolia* Nee, 27-VII-1994, 1 male.

Aphelinus howardii Dalla Torre

CALIFORNIA. ALAMEDA CO.: Albany; *Macrosiphum* (*Sitobion*) *ramni* (Clark) on *Rhamnus californica* Eschscholtz, 4-VIII-1994, 1 female, 1 male.

Aphelinus sp. nr. *mali* (Haldemann)

LOUISIANA. ST. HELENA PAR.: Highway 38, 5 kms. west of Easleyville; *Illinoia lirioidendri*

(Monell) on *Liriodendron tulipifera* L., 29-IV-1992, 4 females.

Aphelinus sp. nr. *perpallidus* Gahan

CALIFORNIA. ALAMEDA CO.: Berkeley; *Periphyllus* sp. on *Acer* sp., 11-VIII-1990, 15 females and 14-VI-1991, 4 females. SONOMA CO.: Petaluma; *I. lirioidendri* on *L. tulipifera*, 29-IV-1992, 1 female (reported as *Aphelinus* sp. in Zuparko and Dahlsten 1993).

Aphelinus sp. nr. *sanborniae* Gahan

CALIFORNIA. ALAMEDA CO.: Berkeley; *Aphis pomi* DeGeer on *Cotoneaster pannosa* Franch, 26-VIII-1993, 1 male.

Aphelinus subflavescens (Westwood)

CALIFORNIA. ALAMEDA CO.: Berkeley; *Eucercaphis gillettei* Davidson on *Alnus* sp., 30-VI-1992, 1 female and 1 male.